BEREND AUKEMA

Biological Station, Wijster (Communication no. 421)

MCZ LIBRARY
JAN 25 1991
HARVARD UNIVERSITY

TAXONOMY, LIFE HISTORY AND DISTRIBUTION OF THREE CLOSELY RELATED SPECIES OF THE GENUS *CALATHUS* (COLEOPTERA: CARABIDAE)

Aukema, B., 1990. Taxonomy, life history and distribution of three closely related species of the genus *Calathus* (Coleoptera: Carabidae). – Tijdschrift voor Entomologie 133: 121-141, figs. 1-18, tabs. 1-15 [ISSN 0040-7496]. Published 14 December 1990.

After cross-breeding experiments between *Calathus melanocephalus*, *C. mollis mollis* and *C. mollis cinctus* and analysis of morphological data of these taxa, *Calathus cinctus* is established as a good species. An identification key for the three species is given, main morphological differences are depicted and data on their biotope, life history, distribution and time trends are provided and discussed.

Berend Aukema, Pomona 66, 6708 CC Wageningen, The Netherlands.

Keywords. – Carabidae; *Calathus*; *cinctus*; *melanocephalus*; *mollis*; cross-breeding; identification key; life history; distribution maps; time trends.

In the past the status of *Calathus melanocephalus* (Linnaeus, 1758) and *C. mollis* (Marsham, 1802) as different species has been questioned many times, mainly because of the frequent occurrence of morphologically intermediate specimens. Schatzmayr (1937), Lindroth (1943) and Wiebes-Rijks (1959) treated them as distinct species, whereas Friederichs (1907) and Gersdorf (1937) could not find any distinguishing character between both taxa at all. Furthermore the existence of a morphologically intermediate form *cinctus* Motschulsky, 1850 (= *erythroderus* Gemminger & Harold, 1868), established as a subspecies of *mollis* by Lindroth (1945), masks the status of these taxa.

This so-called *melanocephalus* group belongs to *Neocalathus*, established as a subgenus of the genus *Calathus* Bonelli by Ball and Negre (1972) with *Calathus melanocephalus* as the type species. For nomenclature in the *melanocephalus* group see Aukema (1990) and Aukema & Luff (1990).

The discovery at Wijster of populations of a *cinctus*-like *Calathus* on abandoned agricultural fields in the surroundings of the Biological Station of the Agricultural University Wageningen (van Dijk 1978) offered a good opportunity for studying its taxonomic relationship with both *melanocephalus* and *mollis*, and its life history.

Moreover, in the present study cross-breeding experiments between these three taxa were carried out to elucidate their taxonomic status. Morphological data (including biometrics) were used to support the resulting classification.

The taxonomic characters given in literature to distinguish *melanocephalus* and *mollis* from each other are:

1. The coloration of the pronotum in comparison to the head (and elytra): clear rufous, contrasting with the black head and elytra in *melanocephalus*, and piceus to brown and not or little contrasting in *mollis*. In the typical form of *melanocephalus* and in *mollis* all appendages are pale. However, a varying degree of melanism may occur in *melanocephalus*, in wich the pronotum is more or less infuscated, from possessing only a faint cloud at the centre to being black with only narrowly translucent margins (in that case also the appendages are melanistic, at least tarsi brown, often also the main part of legs and palpi, as well as middle antennal segments (Jeannel 1942, Lindroth 1974, 1986, Vereshchagina 1985).
2. The shape and size of the right paramere: widened at the tip and hooked at the extreme apex in *melanocephalus* and not widened and unarmed or with a very small hook at the apex in *mollis* (Lindroth 1974, 1986, Freude 1976, Vereshchagina 1985). Differences in internal and external morphology of the vesica are indicated by Lindroth (1943) and Vereshchagina (1985).
3. The dimensions of the metepisterna: short in *melanocephalus* (ca. 1.6 times as long as wide in both brachypterous and macropterous specimens), and longer in macropterous specimens of *mollis* (ca. 1.8 times as long as wide) (Jeannel 1942, Lindroth 1974, Freude 1976, Vereshchagina 1985).

4. The shape of the pronotum: more slender, with the greatest width usually before the middle and clearly narrowed towards the base in *mollis*, and less slender, with the greatest width in or behind the middle and sides less convergent in the basal half in *melanocephalus* (Freude 1976, Lindroth 1986, Vereshchagina 1985).
5. The shape of the elytra: longer oval (more stretched), with lateral margin curved and gradually tapering apically in *mollis*, and shorter oval, with sides almost parallel and broadly rounded apically in *melanocephalus* (Freude 1976, Lindroth 1986).

According to both Lindroth (1974, 1986) and Freude (1976) the subspecies *mollis cinctus* (at the time known as *mollis erythroderus*) can be distinguished from *mollis mollis* by the entirely rufous pronotum, contrasting with the piceus to brown head and elytra. Van Dijk (1978) furthermore mentions a difference in the colour of the sternites between *cinctus* and *melanocephalus*. Material collected in the field was studied to evaluate the usefulness of these characters for identification.

Finally museum collections were revised in order to get an impression of the distribution of the species involved in The Netherlands. Due to misidentification in the past, existing distribution maps of the taxa concerned (Turin, Haeck & Hengeveld 1977) have to be replaced.

In this paper the taxonomic status of the three taxa mentioned above is unravelled and the data presented lead to the conclusion that *Calathus cinctus* can be considered as a good species. Data on habitat, life history and distribution of *cinctus*, *melanocephalus* and *mollis* are given.

Material and methods

Cross-breeding experiments

Single-pair crosses between all possible combinations of the three taxa were carried out during 1978/1979 and 1979/1980 under approximately outside conditions in an outdoor insectary. In 1978/1979 selected pairs were kept either in glass

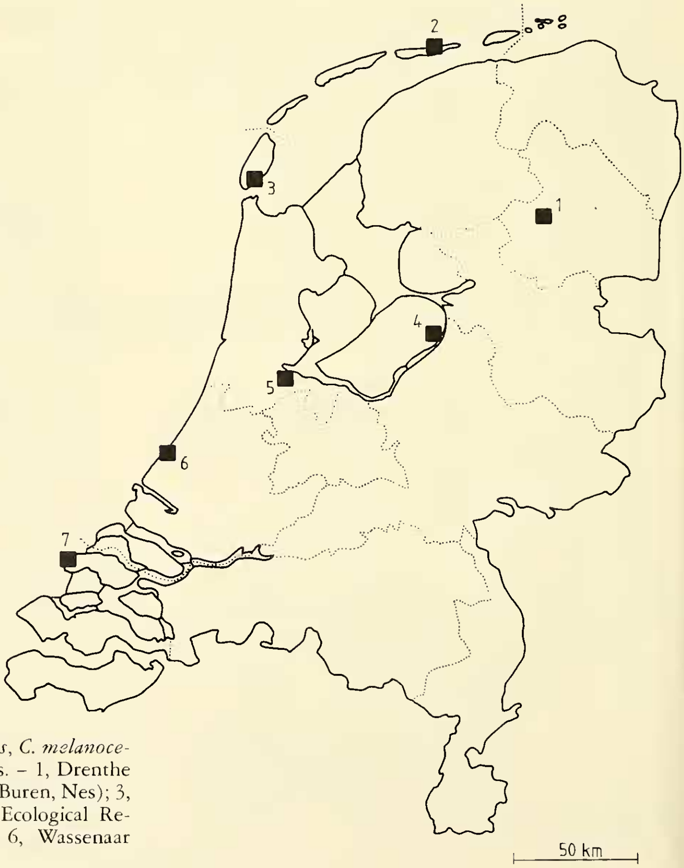


Fig. 1. Collecting sites of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* in The Netherlands. – 1, Drenthe (Dwingeloo, Kraloo, Nuil); 2, Ameland (Buren, Nes); 3, Texel ('t Horntje); 4, Oost-Flevoland (Ecological Reserve); 5, Amsterdam (Bijlmermeer); 6, Wassenaar (Meijendel); 7, Schouwen (Haamstede).

jars on sieved peat litter (group 1) or in petri dishes in ground peat litter (group 2). In the first case newly emerged larvae were gathered from the peat litter as described by van Dijk (1979a), whereas for the second group eggs were separated from the peat according the sieve-wash method of Mols et al. (1981). Eggs were incubated at a constant temperature of 19° C. Larvae were moved to glass tubes in which they were reared individually in peat litter in the outdoor rearing facility. During the winter months (from the end of November until the end of March) the larvae were moved to a climate room at 5°C under short day (LD 10/14) conditions. Single-pair crosses of males and females of the same taxon served as control groups. Crosses and origin of the beetles used are given in table 1.

Offspring of crosses performed by van Dijk (1978) in 1977/1978 and specimens collected in the field before the start of the reproduction period (tenerals in the case of females; *cinctus* from Dwingeloo, *melanocephalus* from Kraloo, and *mollis* from Voorne) were used as starting material (table 1). Furthermore, offspring of females inseminated in the field (*cinctus* from Nuil and Dwingeloo, and *melanocephalus* from Oost-Flevoland) were reared in order to get virgin females as starting material for the next crossing programme.

In 1979/1980 crosses were carried out comparable to those of group 2 of the preceding year. The food, however, was changed from pieces of mealworm to small maggots. Again offspring of females inseminated in the field (*mollis* from the West Frisian Island of Ameland) was reared. Information on these crosses is summarized in table 2. Collecting sites are depicted in fig. 1.

Morphology

Material collected in the field was studied to check the validity and usefulness of characters given in literature for identification of the species concerned. Samples of the following localities were used:
Calathus cinctus: Drenthe: Dwingeloo (Noordenveld), Ruinen (Nuil); Friesland: Ameland (Buren, Nes); N-Holland: Texel ('t Horntje); Zuid-Holland: Wassenaar (Meijendel) and Zeeland: Schouwen (Haamstede).
Calathus melanocephalus: Friesland: Ameland (Buren, Nes); Drenthe: Dwingeloo (Noordenveld), Ruinen (Nuil, Kraloo); Flevoland: Oost-Flevoland (Oecologisch Reservaat); N-Holland: Texel ('t Horntje), Amsterdam (Bijlmermeer).
Calathus mollis: Friesland: Ameland (Buren, Nes); Z-Holland: Wassenaar (Meijendel) and Zeeland: Schouwen (Haamstede).

Measurements were made with a Wild M5 stereo-microscope provided with a calibrated ocular micrometer. The following measurements were taken (magnification between brackets):

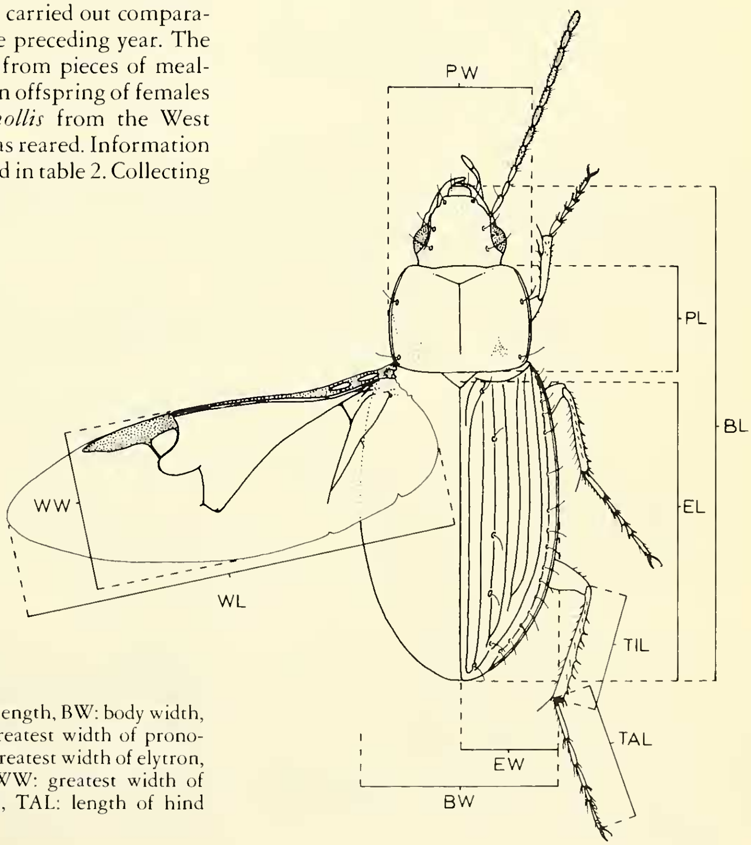


Fig. 2. Measurements. BL: body length, BW: body width, PL: length of pronotum, PW: greatest width of pronotum, EL: length of elytron, EW: greatest width of elytron, WL: greatest length of wing, WW: greatest width of wing, TIL: length of hind tibia, TAL: length of hind tarsus.

Table 1. Single-pair crosses between and within *Calathus cinctus*, *C. melanocephalus* and *C. mollis* in 1978/1979. cin: *cinctus*; mel: *melanocephalus*; mol: *mollis*; lw: long winged; sw: short winged; N: number of crosses; NL: ibid., producing larvae; L: number of larvae produced and reared; LR: number of larvae reared; B: number of beetles reared.

	Parents							
	Species/Wing-morph		Origin					
	Males	Females	Males	Females	N	NL	L	B
Group 1	mel sw	cin lw	Kraloo (28-6-1978)	F_1-offspring 1978 1)	4	–	–	–
	mel sw	cin lw	Kraloo (28-6-1978)	Dwingeloo (19-7-1978, teneral)	1	–	–	–
	mel sw	cin sw	Kraloo (28-6-1978)	F_1-offspring 1978	5	–	–	–
	cin lw	mel sw	F_1-offspring 1978	Kraloo (28-6-1978, tenerals)	5	1	41	–
	cin sw	mel sw	F_1-offspring 1978	Kraloo (28-6-1978, tenerals)	5	1	32	–
Group 2	cin lw	mel sw	Nuil (4-8-1978)	F_1-offspring 1978	6	–	–	–
	cin lw	mel sw	F_1-offspring 1978	F_1-offspring 1978	6	–	–	–
	cin sw	mel sw	Nuil (4-8-1978)	F_1-offspring 1978	2	–	–	–
	cin sw	mel sw	F_1-offspring 1978	F_1-offspring 1978	7	–	–	–
	mol lw	mel lw	Voorne (end July 1978) 2)	F_1-offspring 1978	1	–	–	–
	mol lw	mel sw	Voorne (end July 1978)	F_1-offspring 1978	5	–	–	–
	cin lw	mol lw	Voorne (end July 1978)	Voorne (end July 1978)	5	2	20	–
	mel sw	mol lw	Kraloo (4-8-1978)	Voorne (end July 1978)	5	2	27	–
							LR	
Controls	cin lw	cin lw	Parents 1977 1)	F_1-offspring 1978	6	5	283	179
	cin sw	cin lw	F_1-offspring 1978	Parents 1977	6	5	149	59
		cin lw	no males	Dwingeloo (23-8/22-9-1978)	16	16	734	471
		cin lw	no males	Nuil (23-8/22-9-1978)	5	5	253	158
	cin lw	cin sw	F_1-offspring 1978	Parents 1977	6	4	114	48
	cin sw	cin sw	F_1-offspring 1978	F_1-offspring 1978	6	6	295	182
		cin sw	no males	Dwingeloo (7-9-1978)	1	1	49	27
		cin sw	no males	Nuil (23/31-8-1978)	4	3	147	86
	mel sw	mel sw	Kraloo (30-8-1978)	Kraloo (30-8-1978)	6	6	60	40
		mel lw	no males	O-Flevoland (20-9-1978)	14	13	489	304
		mel sw	no males	O-Flevoland (27-9-1978)	13	10	371	236

1): parents and offspring of crosses carried out by Th. S. van Dijk

2): material collected by A. van Tiggele

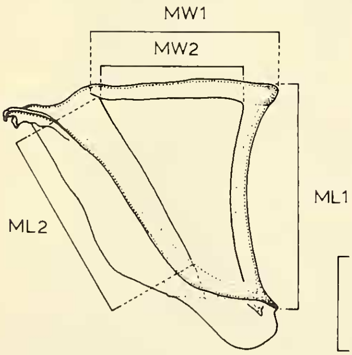


Fig. 3. Measurements of met-episternum. ML1, ML2: length; MW1, MW2: width. Scale 0.5 mm.

- length and width of the body (12): length between tip of mandibles and apex of elytra and greatest width over elytra (fig. 2: BL and BW).
- length and width of the pronotum (25): median length and greatest width (fig. 2: PL and PW).
- length and width of the (right) elytron (12): EL and EW in fig. 2. EW was calculated as half the greatest body-width (0.5*BW).
- length and width of the (right) wing (12): greatest length and greatest width (fig. 2: WL and WW).
- length and width of the (right) met-episternum (50) as shown in fig. 3 (length: ML1, ML2; width: MW1, MW2).
- length of the (right) hind tibia and of the (right) hind tarsus (25) (fig. 2: TIL and TAL).

Elytra, wings, met-episterna and hind-legs were removed from the body for proper measurement in a flat plane. Wings were put on a slide in alcohol and unfolded with a fine brush.

From these measurements ratios between length and width of the body (BL/BW), width and length

Table 2. Single-pair crosses between and within *Calathus cinctus*, *C. melanocephalus* and *C. mollis* (1979/1980). cin: *cinctus*; mel: *melanocephalus*; mol: *mollis*; lw: long winged; sw: short winged; N: number of crosses; E: number of eggs laid; NL: number of crosses producing larvae; L: number of larvae produced and reared; LR: number of larvae reared; B: number of reared beetles.

PARENTS								
Species/Wing-morph		Origin						
Males	Females	Males	Females	N	E	NL	L	B
mel lw	cin lw	Oost-Flevoland (11-10-1978)	F_1-offspring 1979	4	422	3	68	–
mel sw	cin lw	F_1-offspring 1979 (O-Flevoland)	F_1-offspring 1979	4	591	–	–	–
mel sw	cin lw	F_1-offspring 1979 (Kraloo)	F_1-offspring 1979	4	320	–	–	–
mel lw	cin sw	Oost-Flevoland (11-10-1978)	F_1-offspring 1979	4	91	–	–	–
mel sw	cin sw	F_1-offspring 1979 (O-Flevoland)	F_1-offspring 1979	4	219	–	–	–
mel sw	cin sw	F_1-offspring 1979 (Kraloo)	F_1-offspring 1979	4	201	–	–	–
mol lw	cin lw	Ameland (28-6-1979)	F_1-offspring 1979	4	184	–	–	–
mol lw	cin sw	Ameland (28-6-1979)	F_1-offspring 1979	4	254	–	–	–
cin lw	mel lw	F_1-offspring 1979	Oost-Flevoland (25-10-1978)	2	59	–	–	–
cin lw	mel lw	Ameland (28-6-1979)	Oost-Flevoland (25-10-1978)	2	216	–	–	–
cin sw	mel lw	F_1-offspring 1979	Oost-Flevoland (25-10-1978)	2	229	–	–	–
cin sw	mel lw	Ameland (28-6-1979)	Oost-Flevoland (25-10-1978)	2	418	1	173	–
cin lw	mel sw	F_1-offspring 1979	F_1-offspring 1979 (O-Flevoland)	2	23	–	–	–
cin lw	mel sw	Ameland (28-6-1979)	F_1-offspring 1979 (O-Flevoland)	2	58	–	–	–
cin lw	mel sw	F_1-offspring 1979	F_1-offspring 1979 (Kraloo)	2	218	2	77	–
cin lw	mel sw	Ameland (28-6-1979)	F_1-offspring 1979 (Kraloo)	2	14	–	–	–
cin sw	mel sw	F_1-offspring 1979	F_1-offspring 1979 (O-Flevoland)	2	15	–	–	–
cin sw	mel sw	Ameland (28-6-1979)	F_1-offspring 1979 (O-Flevoland)	2	50	1	26	–
cin sw	mel sw	F_1-offspring 1979	F_1-offspring 1979 (Kraloo)	2	87	–	–	–
cin sw	mel sw	Ameland (28-6-1979)	F_1-offspring 1979 (Kraloo)	2	4	–	–	–
mol lw	mel lw	Ameland (28-6-1979)	Oost-Flevoland (25-10-1978)	4	181	1	25	–
mol lw	mel sw	Ameland (28-6-1979)	F_1-offspring 1979 (O-Flevoland)	4	57	–	-	–
mol lw	mel sw	Ameland (28-6-1979)	F_1-offspring 1979 (Kraloo)	4	59	–	–	–
Control groups							LR	
mel lw	mel lw	F_1-offspring 1979	F_1-offspring 1979	4	1173	4	238	85
mel sw	mel lw	F_1-offspring 1979 (O-Flevoland)	F_1-offspring 1979	4	1084	4	240	135
mel sw	mel lw	F_1-offspring 1979 (Kraloo)	F_1-offspring 1979	4	1279	4	217	139
mel lw	mel sw	F_1-offspring 1979	F_1-offspring 1979 (O-Flevoland)	4	1113	4	239	92
mel sw	mel sw	F_1-offspring 1979 (O-Flevoland)	F_1-offspring 1979 (O-Flevoland)	4	959	4	240	130
mel sw	mel sw	F_1-offspring 1979 (Kraloo)	F_1-offspring 1979 (O-Flevoland)	4	665	4	224	136
mel lw	mel sw	F_1-offspring 1979	F_1-offspring 1979 (Kraloo)	4	682	4	160	96
mel sw	mel sw	F_1-offspring 1979 (O-Flevoland)	F_1-offspring 1979 (Kraloo)	4	1079	4	240	132
mel sw	mel sw	F_1-offspring 1979 (Kraloo)	F_1-offspring 1979 (Kraloo)	4	920	4	240	112
cin lw	cin lw	F_1-offspring 1979	F_1-offspring 1979	2	468	2	120	43
cin lw	cin lw	Ameland (28-6-1979)	F_1-offspring 1979	1	232	1	60	20
cin sw	cin lw	F_1-offspring 1979	F_1-offspring 1979	2	639	2	85	41
cin sw	cin lw	Ameland (28-6-1979)	F_1-offspring 1979	1	509	1	60	13
cin lw	cin sw	F_1-offspring 1979	F_1-offspring 1979	2	496	2	116	68
cin lw	cin sw	Ameland (28-6-1979)	F_1-offspring 1979	1	216	1	60	20
	mol lw	no males	Ameland (28-6-1979)	28	573	9	309	194

of the pronotum (PW/PL), pronotum width and body width (PW/BW), length and width of the elytra (EL/EW), length of the elytra and body length (EL/BL), length and width of the wings (WL/WW), wing-length and length of the elytra (WL/EL), length and width of the met-episterna (ML2/MW2), and the ratio between the lengths of the hind tarsus and hind tibia (TAL/TIL) were estimated.

Special attention was paid to the coloration of the beetles, the size and shape of the right paramere and to the number of dorsal punctures in the third elytral interval.

Habitat and life history

Details of the habitat and the life history of the species were derived from the analysis of field data (mixed populations of *cinctus* and *melanocephalus* from Dwingeloo, Ruinen and the West Frisian Island of Texel and populations of *cinctus* and *mollis* from the West Frisian Island of Ameland), from literature (populations of *melanocephalus* studied by Vlijm & van Dijk (1967), Vlijm et al. (1968) and van Dijk (1972, 1973)) and from breeding experiments with the three species under outside conditions carried out in 1981/1982 and 1982/1983.

Distribution

Calathus-material of this group from Dutch collections was revised to be able to get an impression of the distribution of the species in The Netherlands. Material from the following collections is included:

Museums and institutions: Zoölogisch Museum, Amsterdam; Rijksmuseum van Natuurlijke Historie, Leiden; Vakgroep Entomologie, Landbouwuniversiteit, Wageningen; Biologisch Station, Landbouwuniversiteit, Wijster.

Private collections: K. den Bieman, Bennekom; E. H. M. Bouvy, Beek; H. T. Edzes, Nijmegen; T. van Gijzen, Arnhem; Th. Heijerman, Wageningen; S. van Heijnsbergen, Naarden; Y. Jongema, Wageningen and A. P. J. A. Teunissen, Vlijmen.

Additional material was supplied by K. Alders, Arnhem; M. A. Baars, De Koog, Texel (Loopkeverwerkgroep Texel); Th. S. van Dijk, Wijster; P. J. M. Mols, Heteren and H. Turin, Renkum.

Time trends in the occurrence of the species (i. e. numbers of occupied 10 × 10 km squares of the distribution maps per decade since 1870) were estimated according to the method of Turin & den Boer (1988).

RESULTS

Cross-breeding experiments

In total 123 single-pair crosses were carried out: 59 between *cinctus* and *melanocephalus*, 47 between *cinctus* and *mollis* and 17 between *melanocephalus* and *mollis* (tables 1 and 2). None of these crosses produced adult offspring although in 5 (8.5 %), 3 (6.4 %) and 3 (17.6 %) cases respectively larvae were produced, which, however, never reached the third larval stage.

Table 3. Measurements (in mm) of short winged males of *Calathus cinctus* and *C. melanocephalus* from Texel. N: number of measurements.

		cinctus			*melanocephalus*		
	MEASUREMENT	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	20	6.79	6.59-6.98	20	6.66	6.51-6.82
	Width (BW)	20	2.71	2.64-2.77	20	2.67	2.61-2.73
	BL/BW	20	2.51	2.47-2.55	20	2.50	2.45-2.55
Pronotum	Length (PL)	20	1.64	1.61-1.68	20	1.68	1.65-1.72
	Width (PW)	20	1.99	1.95-2.04	20	2.11	2.06-2.15
	PW/PL	20	1.21	1.20-1.23	20	1.25	1.23-1.27
	PW/BW	20	0.74	0.73-0.74	20	0.79	0.78-0.80
Elytron	Length (EL)	20	4.18	4.07-4.29	20	4.09	4.00-4.18
	Width (EW)	20	1.35	1.32-1.38	20	1.33	1.30-1.36
	EL/EW	20	3.09	3.05-3.12	20	3.07	3.03-3.11
	EL/BL	20	0.62	0.61-0.62	20	0.61	0.60-0.63
Wing	Length (WL)	20	1.93	1.85-2.01	20	1.93	1.86-2.00
	Width (WW)	20	0.48	0.45-0.51	20	0.51	0.47-0.54
	WL/WW	20	4.05	3.86-4.24	20	3.86	3.65-4.07
	WL/EL	20	0.46	0.45-0.47	20	0.47	0.46-0.49
Met-episternum	Length (ML2)[1])	20	0.76	0.74-0.78	20	0.70	0.68-0.73
	Width (MW2)[1])	20	0.57	0.55-0.59	20	0.57	0.55-0.58
	ML2/MW2 (ME2)	20	1.34	1.32-1.36	20	1.24	1.22-1.27
Hindleg	Length tarsus (TAL)	20	2.07	2.01-2.13	20	2.02	1.98-2.06
	Length tibia (TIL)	20	2.02	1.98-2.07	20	1.98	1.94-2.01
	TAL/TIL	20	1.02	1.01-1.03	20	1.02	1.01-1.04

[1]): see fig. 3.

All control crosses (42 of *melanocephalus* and 30 of *cinctus*) crosses that produced larvae (respectively 100 % and 82 % for both years together), also produced adult offspring (tables 1 and 2). In 1979/1980 all crosses of both species produced offspring (table 2). In the case of *mollis* not sufficient material to carry out control crosses in the same way was available. However, of 28 females collected in the field (Ameland, Buren, 28.vi.1979) and kept without males under the same conditions as single-pair crosses, 9 produced larvae and offspring (table 2: 194 beetles from 309 larvae). The other 19 females (ten of which were tenerals at the time of capture) produced no or only a few unfertilized eggs, and were considered not to have been inseminated at all. Nevertheless it is clear from these results that also in the case of *mollis* the failure of single-pair crosses with *cinctus* and *melanocephalus* cannot be attributed to the rearing conditions used.

In 1979/1980 egg production was also estimated. It appeared that, although unfertilized females may produce a considerable number of eggs, the egg production of fertilized females generally is much higher (table 2). It is concluded that *cinctus*, *melanocephalus* and *mollis* show mutual reproductive isolation, and, therefore, have to be considered as distinct species.

Morphology

Biometric data, especially the ratio length/width of the met-episterna, have been used in attempts to separate the taxa of this group of closely related species (Gersdorf 1937, Wiebes-Rijks 1959). The establishment of *cinctus* as a valid species as the result of the breeding program necessitated a new attempt to find morphological differences between the three species. Concerning biometrics, however, two points have to be taken into account. Firstly general differences both between sexes (on average females are larger than males) and between wing-morphs (on average long winged specimens are larger than short winged specimens and differently shaped) exist in these species. Secondly, the way measurements are made should be described (and figured) in detail, which apparently is not normal practice. Lindroth (1974) and Freude (1976), for instance, use the ratio length/width of the met-episterna without indicating how to measure it, and do not point out the differences between sexes and between wing-morphs in a proper way.

Tables 3-6 list measurements and ratio's of both males and females of short as well as long winged *Calathus cinctus* and *C. melanocephalus* collected on Texel by M. A. Baars and of long winged *C. mollis* collected in the coastal dunes near Haam-

Table 4. Measurements (in mm) of short winged females of *Calathus cinctus* and *C. melanocephalus* from Texel. N: number of measurements.

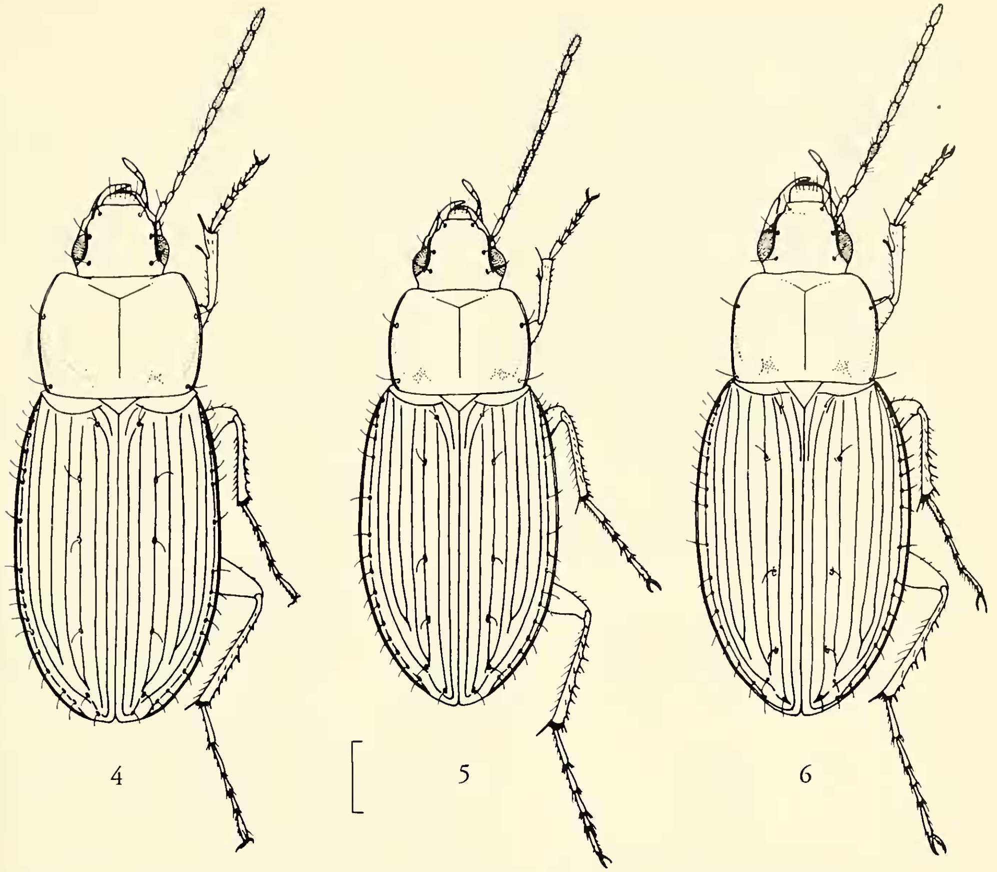
		cinctus			*melanocephalus*		
	MEASUREMENT	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	20	7.39	7.23-7.56	20	7.32	7.18-7.46
	Width (BW)	20	3.01	2.94-3.09	20	2.95	2.91-3.00
	BL/BW	20	2.46	2.42-2.50	20	2.48	2.44-2.52
Pronotum	Length (PL)	20	1.77	1.73-1.81	20	1.79	1.76-1.82
	Width (PW)	20	2.19	2.13-2.24	20	2.28	2.24-2.32
	PW/PL	20	1.23	1.22-1.25	20	1.27	1.26-1.28
	PW/BW	20	0.73	0.72-0.74	20	0.77	0.76-0.78
Elytron	Length (EL)	20	4.54	4.44-4.64	20	4.45	4.36-4.53
	Width (EW)	20	1.51	1.47-1.54	20	1.48	1.46-1.50
	EL/EW	20	3.02	2.98-3.05	20	3.01	2.97-3.04
	EL/BL	20	0.61	0.61-0.62	20	0.61	0.60-0.62
Wing	Length (WL)	20	2.14	2.08-2.20	20	2.06	1.99-2.13
	Width (WW)	20	0.60	0.57-0.62	20	0.60	0.55-0.64
	WL/WW	20	3.61	3.48-3.75	20	3.49	3.32-3.65
	WL/EL	20	0.47	0.46-0.48	20	0.46	0.45-0.48
Met-episternum	Length (ML2)	20	0.83	0.80-0.85	20	0.76	0.74-0.77
	Width (MW2)	20	0.64	0.62-0.65	20	0.62	0.61-0.64
	ML2/MW2 (ME2)	20	1.30	1.27-1.33	20	1.22	1.20-1.24
Hindleg	Length tarsus (TAL)	20	2.08	2.03-2.12	20	1.97	1.92-2.01
	Length tibia (TIL)	20	2.07	2.03-2.12	20	2.02	1.98-2.06
	TAL/TIL	20	1.00	0.99-1.02	20	0.97	0.96-0.98

Table 5. Measurements (in mm) of long winged males of *Calathus cinctus* and *C. melanocephalus* from Texel and *C. mollis* from Haamstede. N: number of measurements.

		cinctus			*melanocephalus*			*mollis*		
	Measurement	N	Mean	95% c.l.	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	11	6.78	6.52-7.03	7	7.19	6.93-7.46	20	7.34	7.18-7.50
	Width (BW)	11	2.64	2.55-2.73	7	2.85	2.77-2.94	20	2.79	2.73-2.85
	BL/BW	11	2.57	2.52-2.62	7	2.52	2.44-2.60	20	2.63	2.61-2.66
Pronotum	Length (PL)	11	1.60	1.54-1.65	7	1.77	1.70-1.83	20	1.65	1.61-1.69
	Width (PW)	11	1.92	1.85-1.99	7	2.24	2.17-2.31	20	2.05	2.00-2.09
	PW/PL	11	1.20	1.18-1.23	7	1.27	1.25-1.29	20	1.24	1.23-1.25
	PW/BW	11	0.73	0.72-0.74	7	0.79	0.78-0.79	20	0.73	0.73-0.74
Elytron	Length (EL)	11	4.12	3.98-4.25	7	4.32	4.19-4.45	20	4.38	4.27-4.49
	Width (EW)	11	1.32	1.27-1.36	7	1.43	1.38-1.47	20	1.39	1.36-1.42
	EL/EW	11	3.12	3.07-3.18	7	3.03	2.98-3.09	20	3.14	3.11-3.18
	EL/BL	11	0.61	0.59-0.63	7	0.60	0.58-0.62	20	0.60	0.59-0.60
Wing	Length (WL)	11	6.26	5.89-6.62	7	7.10	6.86-7.85	20	6.61	6.39-6.83
	Width (WW)	11	2.36	2.23-2.50	7	2.68	2.63-2.74	20	2.46	2.37-2.54
	WL/WW	11	2.65	2.53-2.77	7	2.65	2.58-2.72	20	2.69	2.66-2.73
	WL/EL	11	1.52	1.47-1.57	7	1.64	1.62-1.67	20	1.51	1.49-1.53
Met-episternum	Length (ML2)	11	0.77	0.74-0.79	7	0.77	0.73-0.81	20	0.82	0.80-0.84
	Width (MW2)	11	0.57	0.55-0.59	7	0.60	0.58-0.62	20	0.58	0.56-0.59
	ML2/MW2 (ME2)	11	1.35	1.31-1.39	7	1.28	1.21-1.35	20	1.43	1.40-1.45
Hindleg	Length tarsus (TAL)	11	2.01	1.93-2.09	6	2.18	2.11-2.24	20	2.19	2.14-2.25
	Length tibial (TIL)	11	1.96	1.90-2.03	6	2.13	2.04-2.22	20	2.09	2.04-2.15
	TAL/TIL	11	1.02	1.01-1.04	6	1.02	1.00-1.05	20	1.05	1.04-1.06

Table 6. Measurements (in mm) of long winged females: *Calathus cinctus* and *C. melanocephalus* from Texel and *C. mollis* from Haamstede. N: number of measure-ments.

		cinctus			*melanocephalus*			*mollis*		
	Measurement	N	Mean	95% c.l.	N	Mean	95% c.l.	N	Mean	95% c.l.
Body	Length (BL)	11	7.04	6.78-7.30	20	7.85	7.72-7.97	20	8.03	7.86-8.19
	Width (BW)	11	2.87	2.74-3.00	20	3.15	3.12-3.18	20	3.18	3.10-3.25
	BL/BW	11	2.46	2.41-2.51	20	2.49	2.45-2.54	20	2.53	2.51-2.55
Pronotum	Length (PL)	11	1.67	1.60-1.74	20	1.89	1.86-1.92	20	1.77	1.74-1.81
	Width (PW)	11	2.09	1.99-2.20	20	2.43	2.40-2.47	20	2.28	2.22-2.34
	PW/PL	11	1.26	1.23-1.28	20	1.29	1.27-1.31	20	1.28	1.27-1.30
	PW/BW	11	0.73	0.72-0.74	20	0.77	0.76-0.78	20	0.72	0.71-0.72
Elytron	Length (EL)	11	4.34	4.18-4.50	20	4.80	4.72-4.88	20	4.81	4.71-4.92
	Width (EW)	11	1.43	1.37-1.50	20	1.57	1.56-1.59	20	1.59	1.55-1.62
	EL/EW	11	3.03	2.98-3.08	20	3.05	3.00-3.09	20	3.03	3.01-3.06
	EL/BL	11	0.62	0.61-0.63	20	0.61	0.60-0.62	20	0.60	0.60-0.60
Wing	Length (WL)	11	6.49	6.15-6.82	20	7.51	7.38-7.65	20	7.27	7.07-7.46
	Width (WW)	11	2.51	2.38-2.64	20	2.83	2.77-2.89	20	2.77	2.68-2.85
	WL/WW	11	2.58	2.52-2.64	20	2.65	2.62-2.69	20	2.63	2.60-2.65
	WL/EL	11	1.49	1.45-1.54	20	1.57	1.54-1.59	20	1.51	1.49-1.52
Met-episternum	Length (ML2)	11	0.82	0.77-0.88	20	0.83	0.81-0.84	20	0.92	0.88-0.94
	Width (MW2)	11	0.61	0.58-0.63	20	0.68	0.66-0.69	20	0.65	0.63-0.66
	ML2/MW2 (ME2)	11	1.36	1.31-1.41	20	1.22	1.21-1.24	20	1.42	1.39-1.45
Hindleg	Length tarsus (TAL)	11	2.00	1.89-2.06	20	2.09	2.06-2.11	20	2.21	2.16-2.25
	Length tibial (TIL)	11	1.97	1.92-2.08	20	2.18	2.15-2.22	20	2.19	2.15-2.23
	TAL/TIL	11	1.01	0.99-1.04	20	0.96	0.94-0.97	20	1.01	1.00-1.02



Figs. 4-6. Habitus of females of *Calathus*. – 4, *C. melanocephalus*; 5, *C. cinctus*; 6, *C. mollis*. Scale 1 mm.

stede (Province of Zeeland) by the author. The following conclusion can be drawn. Although there are some differences between the means (e. g. in the case of the ratio length/width of the metepisterna), these measurements (or ratios estimated from them) do not allow unambiguous identification due to significant individual variation and wide overlap in the ranges of measurements.

Table 7 summarizes length/width ratios (ME1: ML1/MW1 and ME2: ML2/MW2, see fig. 3) of long and short winged males and females of *cinctus* and *melanocephalus*, as well as of long winged males and females of *mollis* (all specimens collected or reared of the latter species turned out to be long winged) from localities mentioned above, as well as from a number of other localities too.

Although both ratios show a clear trend *melanocephalus* <*cinctus*< *mollis* for both males and females, the mutual overlap is so wide that identification on the basis of these ratios alone usually will not be possible. The observed differences between wing-morphs and sexes are smaller than those between species (table 7). In general differences between species, wing-morphs and sexes are better illustrated by ratio ME2 than by ratio ME1.

Table 8 illustrates the variation in the number of dorsal punctures in the 3rd elytral interval of *cinctus* and *melanocephalus* from Texel and *mollis* from Haamstede. In both sexes and wing-morphs of *cinctus* considerable deviation (> 50 %) from the standard number of three punctures in the third elytral interval was found, whereas the deviation in *melanocephalus* and *mollis* was relatively low (< 40 %). Both the number and position of the punctures are also rather variable and certainly not of diagnostic value.

General coloration, shape of the elytra and shape of the right parameres are very constant and can be used to identify most specimens according to the key presented hereafter. Only a few long winged females of *cinctus* and *mollis* may give some problems in identification.

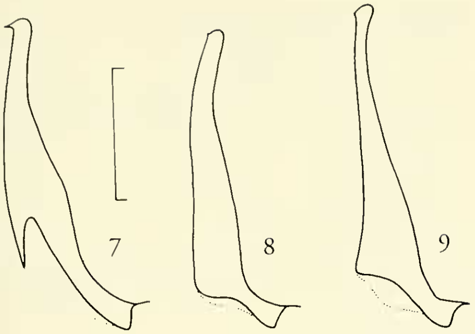
Table 7. Measurements of met-episterna: ratio length/width. ME1: ML1/MW1; ME2: ML2/MW2 (see fig. 3); sw: short winged; lw: long winged; N: Number of measurements.

MALES				ME1			ME2		
Wing-morph	Species	Locality	N	Range	Mean	95% c.l.	Range	Mean	95% c.l.
sw	*cinctus*	Nuil	30	1.06-1.18	1.11	1.10-1.12	1.28-1.46	1.36	1.35-1.38
		Noordenveld[1])	27	1.03-1.22	1.11	1.09-1.13	1.19-1.47	1.34	1.31-1.37
		Texel	20	0.97-1.10	1.04	1.03-1.06	1.25-1.43	1.34	1.32-1.36
sw	*melanocephalus*	Oost-Flevoland	30	0.99-1.16	1.07	1.05-1.08	1.19-1.39	1.29	1.27-1.31
		Nuil	19	0.96-1.10	1.04	1.02-1.06	1.15-1.31	1.23	1.21-1.25
		Noordenveld[1])	30	0.94-1.10	1.03	1.02-1.05	1.10-1.39	1.25	1.23-1.28
		Kraloo	9	0.98-1.10	1.04	1.01-1.06	1.16-1.29	1.24	1.20-1.28
		Bijlmermeer	17	1.03-1.14	1.07	1.06-1.09	1.23-1.40	1.27	1.25-1.30
		Texel	20	0.95-1.07	1.02	1.00-1.03	1.15-1.32	1.24	1.22-1.27
lw	*cinctus*	Nuil	30	1.02-1.19	1.12	1.11-1.13	1.27-1.47	1.39	1.37-1.41
		Noordenveld[1])	30	1.04-1.26	1.14	1.12-1.16	1.18-1.57	1.37	1.33-1.40
		Texel	11	1.00-1.11	1.07	1.05-1.09	1.28-1.46	1.35	1.31-1.39
lw	*melanocephalus*	Oost-Flevoland	13	1.00-1.15	1.08	1.05-1.11	1.14-1.34	1.24	1.21-1.28
		Kraloo	2	1.09-1.12			1.39-1.45		
		Bijlmermeer	3	1.07-1.09			1.21-1.29		
		Texel	7	1.00-1.09	1.05	1.02-1.08	1.20-1.40	1.28	1.21-1.35
lw	*mollis*	Meijendel	14	1.15-1.25	1.19	1.18-1.21	1.33-1.52	1.43	1.40-1.47
		Haamstede	20	1.11-1.20	1.16	1.14-1.17	1.35-1.54	1.43	1.40-1.45
FEMALES									
sw	*cinctus*	Nuil	29	1.02-1.18	1.11	1.09-1.12	1.24-1.49	1.35	1.33-1.37
		Noordenveld[1])	29	1.00-1.20	1.08	1.07-1.10	1.17-1.44	1.30	1.28-1.33
		Texel	20	0.92-1.07	1.01	0.99-1.02	1.14-1.30	1.30	1.27-1.33
sw	*melanocephalus*	Oost-Flevoland	30	0.98-1.16	1.05	1.04-1.07	1.12-1.35	1.25	1.22-1.27
		Nuil	30	1.00-1.10	1.04	1.03-1.05	1.14-1.39	1.25	1.23-1.27
		Noordenveld[1])	30	0.98-1.22	1.06	1.04-1.09	1.16-1.39	1.27	1.24-1.29
		Kraloo	12	1.00-1.13	1.05	1.03-1.08	1.18-1.37	1.24	1.18-1.30
		Bijlmermeer	10	0.98-1.18	1.09	1.05-1.12	1.23-1.33	1.27	1.24-1.30
		Texel	20	0.92-1.07	1.01	0.99-1.02	1.14-1.30	1.22	1.20-1.24
lw	*cinctus*	Nuil	30	1.07-1.21	1.12	1.11-1.13	1.26-1.44	1.35	1.34-1.37
		Noordenveld[1])	29	0.98-1.30	1.13	1.11-1.16	1.24-1.58	1.36	1.33-1.39
		Texel	11	1.05-1.17	1.11	1.08-1.14	1.25-1.49	1.36	1.31-1.41
lw	*melanocephalus*	Oost-Flevoland	30	0.97-1.13	1.06	1.04-1.07	1.12-1.41	1.26	1.24-1.28
		Kraloo	18	0.98-1.18	1.08	1.05-1.11	1.17-1.48	1.30	1.25-1.34
		Bijlmermeer	7	1.03-1.12	1.08	1.05-1.12	1.25.1.43	1.31	1.26-1.37
		Texel	20	0.95-1.08	1.03	1.01-1.04	1.17-1.30	1.22	1.21-1.24
lw	*mollis*	Meijendel	17	1.13-1.28	1.19	1.17-1.21	1.33-1.54	1.43	1.40-1.46
		Haamstede	20	1.05-1.24	1.16	1.15-1.18	1.29-1.61	1.42	1.39-1.45

[1]): measurements M. G. J. Oude Wesselink

Tabel 8. Number of punctures in 3rd elytral striae. N: number of observations; D: deviation (%) from standard number of puntures (3/3) in third striae; sw: short winged; lw: long winged.

				Punctures in 3rd elytral stria (right/left elytrum)											
Species	Sex	Wing morph	N	2/2	2/3	2/4	3/2	3/3	3/4	4/3	4/4	4/5	5/3	5/4	D
cinctus	males	sw	20	–	1	–	–	9	5	2	3	–	–	–	55.0
		lw	11	–	–	–	–	5	3	2	1	–	–	–	54.5
	females	sw	20	–	2	–	–	2	5	5	5	–	1	1	90.0
		lw	11	–	–	–	–	4	2	1	3	–	1	–	63.6
melanocephalus	males	sw	20	–	–	–	–	13	1	4	2	–	–	–	35.0
		lw	7	–	–	–	–	5	2	–	–	–	–	–	28.6
	females	sw	20	–	–	–	–	13	3	3	1	–	–	–	35.0
		lw	20	–	–	–	–	14	3	2	1	–	–	–	30.0
mollis	males	lw	20	1	2	–	–	17	–	–	–	–	–	–	15.0
	females	lw	20	1	1	1	–	13	11	1	1	–	–	–	35.0



Figs. 7-9. Right parameres of *Calathus*. – 7, *C. melanocephalus*; 8, *C. cinctus*; 9, *C. mollis*. Scale 0.5 mm.

In all three species the females are less shining than the males, due to a denser microsculpture of usually isodiametric meshes, which is most obvious on the elytra.

Key to the species

1. Elytra bicoloured, with epipleura, base and dorsal punctures clear rufous, contrasting with the black dorsal surface. Sides of elytra almost parallel and broadly rounded apically (fig. 4). Pronotum more or less rufous, clearly contrasting with the black head and with the elytral surface. Sternites dark, contrasting with the rufous meso- and meta-thoracical structures. Males: right paramere widened and hooked at the tip (fig. 7). Vesica: fig. 10. Wings reduced or fully developed (rarely specimens with only one fully developed wing are found) (body length 6-8 mm) .... *melanocephalus*

– Elytra unicoloury rufous to piceus brown, with sides evenly rounded (figs. 5-6). Little or no contrast in colour between pronotum and head and elytra, nor between sternites and meso- and meta-thorax. Males: right paramere not widened near the apex and unarmed or with a very small hook apically (figs. 8-9) 2

2. Pronotum slightly contrasting with the darker head and the elytra. Males: right paramere hooked, tip unarmed or nearly so (fig. 8). Vesica: fig. 11. Wings either fully developed or strongly reduced (body length 6-8.5 mm) .... *cinctus*

– Pronotum not contrasting with the head and the elytra. Males: right paramere almost straight with a very small hook apically (fig.9). Vesica: fig. 12. Wings always full (body length 6.5-9 mm) .... *mollis*

Habitat and life history

Habitat

Calathus melanocephalus is mainly a species of open country, where it lives on different kinds of moderately dry soil with sparse vegetation, achieving its greatest abundance on sandy soils. It is a common inhabitant of dry meadows, grassland dunes and heaths; also on agricultural land and in thin forest, mainly of *Pinus* (Lindroth 1986) or *Betula* (den Boer pers. comm.). Den Boer (1977) in his subdivision of carabids in habitat groups classified *melanocephalus* as an F-species, i.e. mainly a species of heath and peat moor.

Calathus cinctus is mainly found in mixed populations with the preceding and/or the following species in dry meadows, dune grassland, agricultural land and waste land. Van Dijk (1986) classified *cinctus* as an H-species sensu den Boer (1977), i.e. an eurytopic species, which in most cases prefer localities significantly influenced by human activities (arable fields, pastures, farm yards, gardens and

Figs. 10-12. Vesica of *Calathus*. – 10, *C. melanocephalus*; 11, *C. cinctus*; 12, *C. mollis*. Scale 0.5 mm.

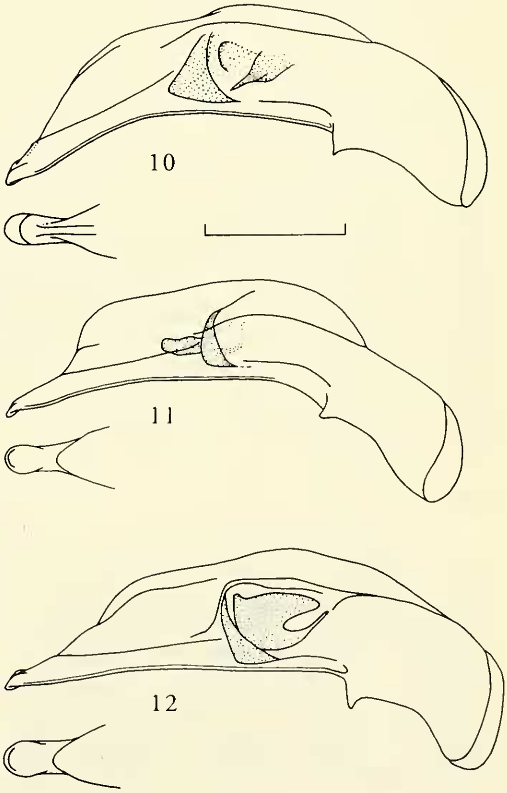


Table 9. Numbers and ratio of *Calathus cinctus* (cin) and *C. melanocephalus* (mel) in mixed populations.

	Nuil			Schoongelegen			Texel		
	Species			Species			Species		
Year	cin	mel	%cin	cin	mel	%cin	cin	mel	%cin
1973	11	30	26.8	8	71	10.1			
1974	13	29	31.0	3	54	5.3			
1975	35	64	35.4	6	23	20.7			
1976	16	20	44.4	22	39	36.1			
1977	34	24	58.6	39	31	55.7			
1978	59	67	46.8	172	112	60.6			
1979	12	34	26.1	3	62	4.6			
1980	2	19	9.5	–	40	–			
1981	–	16	–	–	30	–			
1982	–	6		–	72	–			
1983	1	–		–	84	–			
1984	–	6		–	50	–	82	19	81.1
1985	–	4		–	91	–	264	265	49.9
1986	–	18		–	102	–	133	310	30.0
1987							32	176	15.3
1988							6	74	7.5
Total	183	337		253	861		517	844	

Table 10. Weekly catches of *Calathus cinctus* and *C. melanocephalus* at Nuil, Drenthe in 1976. N: number of beetles; ND: number of females dissected; MNE: mean number of eggs in the ovaries of dissected females.

	cinctus						*melanocephalus*					
	Males	Females					Males	Females				
Date	N	N	ND	Young	Old	MNE	N	N	ND	Young	Old	MNE
7 Jul							1	1	1	1	–	11.0
14 Jul							5	4	4	3	1	4.3
21 Jul	-	1	1	1	–	–	8	12	8	6	2	11.1
28 Jul	-	–	–	–	–	–	14	18	10	9	1	15.9
4 Aug	-	1	1	1	–	15.0	7	10	9	8	1	14.4
11 Aug	-	–	–	–	–	–	11	25	11	7	4	21.5
18 Aug	1	2	2	2	–	23.0	35	26	10	7	3	22.6
25 Aug	3	2	2	1	1	35.0	46	17	10	9	1	23.0
1 Sep	13	15	15	7	8	20.2	42	34	10	8	2	25.8
8 Sep	10	16	16	9	7	33.9	11	24	10	10	–	21.5
15 Sep	21	20	20	15	5	26.5	18	21	10	10	–	17.6
22 Sep	27	18	18	16	2	17.8	23	18	13	12	1	18.8
29 Sep	16	8	8	5	3	18.3	22	4	4	3	1	10.8
6 Oct	17	10	10	9	1	15.4	9	2	2	0	2	16.5
13 Oct	12	20	18	10	8	11.2	6	10	10	9	1	2.0
20 Oct	4	6	6	4	2	9.8	2	1	1	1	–	–
27 Oct	2	6	6	3	3	8.0	2	4	2	2	–	–
3 Nov	–	1	1	1	–	–	1	–	–			
10 Nov	2	3	1	1	–	–	3	1	–			
Total	128	129	125	85	40		262	231	125	105	20	

roadside verges). In three cases a mixed population of *cinctus* and *melanocephalus* was observed during a period of several years: populations at Nuil and Dwingeloo (fields withdrawn from agricultural practice) and at the West Frisian Island of Texel (artificial dune grassland) (table 9). In all three cases, however, *cinctus* disappeared or nearly disappeared after a number of years of coexistence with *melanocephalus*. These data might suggest that *cinctus* is better adapted to changing, unstable habitats than *melanocephalus*. At Nuil and Dwingeloo the treatments for impoverishing the amount of nutrients (annual mowing and removal of vegetation) most likely caused the decrease of *cinctus* (see also van Dijk 1986), while on the dune grassland at Texel a similar treatment might be responsible for the same kind of shift.

Calathus mollis is strictly confined to dry sandy habitats in open country. It lives in sparse xerophilous vegetation, common on sand dunes along the coast, where it occurs in tufts of *Elymus* and *Ammophila* in company with *Demetrias monostigma* Samouelle and *Dromius linearis* (Olivier) (Lindroth 1986; own observations), and only incidentally inland, e.g. on blown sands and other large sand deposits. In den Boer's subdivision (1977) *mollis* would be classified as an E-species (species of blown sands). In the coastal dune region as well as in inland blown sands mixed populations of *mollis* and *cinctus* and occasionally with both *cinctus* and *melanocephalus* occur.

Life history

Annual rhytms. – All three species show a similar type of development. They belong to the group of autumn breeders with a thermic hibernation parapause in the larvae and a photoperiodic aestivation parapause in the adults (Thiele 1977). As in most autumn breeders, adults of *melanocephalus* are almost strictly night active (Thiele 1977). Larvae as well as a varying part of the adults overwinter (Lindroth 1986). In northern and alpine areas, however, *melanocephalus* is a semivoltine spring breeder, instead of a univoltine autumn breeder, adapted to the shorter growing season of a cooler climate (Forsskåhl 1972, DeZordo 1979, Refseth 1988). Under these circumstances larvae of *melanocephalus* need almost two years to develop.

Reproduction period and age-composition. – Detailed information about the life history of *melanocephalus* is given by Vlijm & van Dijk (1967), Vlijm et al. (1968) and van Dijk (1972, 1973). Adults emerge in June and July, reproduce from August onwards and a varying part of these beetles hibernate to become active again in May-June, reproducing for the second time from July onwards. The total reproduction period covers the months July, August and September. Vlijm & van Dijk (1967) and Vlijm et al. (1968) estimated the second year category as about one third of the adult population at Schiermonnikoog, but this figure seem to show significant annual and local variation (van Dijk 1972, Baars & van Dijk 1984). Even three and four year old beetles were found by a mark-recapture experiment in a populations of *melanocephalus* (van Dijk 1979b), representing 26.5 and 0.5 % of the total catch during four years respectively.

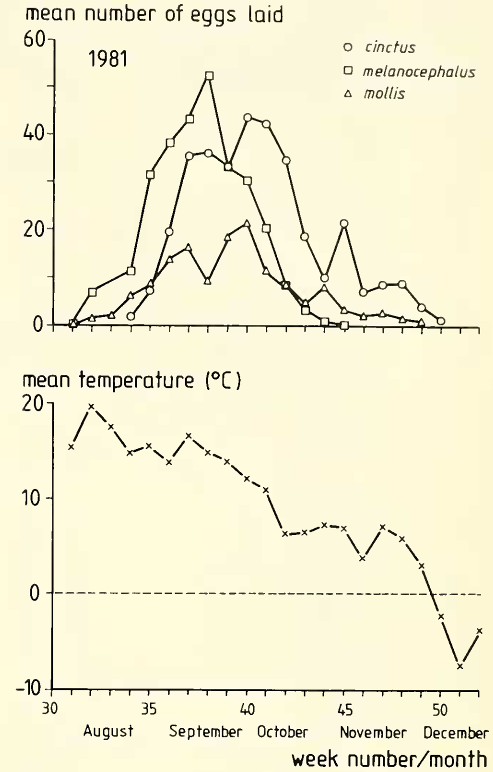


Fig. 13. Mean egg production of *Calathus cinctus* (29 females), *C. melanocephalus* (23 females) and *C. mollis* (16 females) and mean weekly temperature in 1981 under outside conditions.

Calathus cinctus was found to reproduce in Drenthe somewhat later than *melanocephalus* (August-November) (van Dijk 1978). From weekly pitfall samples of *cinctus* collected in 1976 at Nuil, 165 females caught between 21 July and 17 November were dissected and checked for their ovarian development. The main reproductive period, defined

Table 11. Reproduction period of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* in outdoor breeding experiments. N: number of females.

			REPRODUCTION PERIOD			
Year	Species	N	Egg-laying period		Mean number of eggs> 10	
1981	*cinctus*	29	12 Aug – 9 Dec	(18 weeks)	26 Aug – 21 Oct	(9 weeks)
	melanocephalus	36	31 Jul – 6 Nov	(15 weeks)	7 Aug – 9 Oct	(10 weeks)
	mollis	14	3 Aug – 7 Dec	(19 weeks)	31 Aug – 19 Oct	(8 weeks)
1982	*cinctus*	30	16 Aug – 31 Jan	(25 weeks)	30 Aug – 22 Nov	(13 weeks)
	melanocephalus	8	30 Jul – 22 Oct	(13 weeks)	13 Aug – 15 Oct	(10 weeks)
	mollis	17	6 Aug – 3 Jan	(23 weeks)	20 Aug – 5 Nov	(12 weeks)

Table 12. Egg production of *Calathus cinctus*, *C. melanocephalus* and *C. mollis* during the day at a constant temperature of 19° C and approximately natural day length (light period: 6.30-19.00 hours). D: dark period (black); L: light period (white).

			cinctus								*melanocephalus*								*mollis*								
Date	Time	D/L	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	Total
14 Sep 1981	18.30	□																									
(start)		■																									
15 Sep 1981	8.30	□			3		2			2	7	7		6	1	6	13	2	1			3	1				54
		□																									0
	10.30	□					5								9	1											15
	12.30	□															1										1
	14.30	□																									0
	16.30	□																									0
	18.30	□																									0
	20.30	■					1										2	1				2					6
	22.30	■					4							2			6	6				1					19
16 Sep 1981	0.30	■					2				3					1	3	1				3			2	3	18
	2.30	■	5				1											6						1		8	21
	4.30	■	13				2							2											4	2	23
	6.30	■					1									1				3						1	6
	8.30	□																		1			1				2
	10.30	□																					1				1
	12.30	□																									0
		□																									
	18.30	□																									0
		■																									
17 Sep 1981	10.30	□				4	4				14	2		22	13	6	17								4	7	93
		□																									
	18.30	□					3					1										2					6
		■																									
Total			18	0	3	4	25	0	0	2	24	10	0	32	23	15	42	16	1	4	0	11	2	2	10	21	265

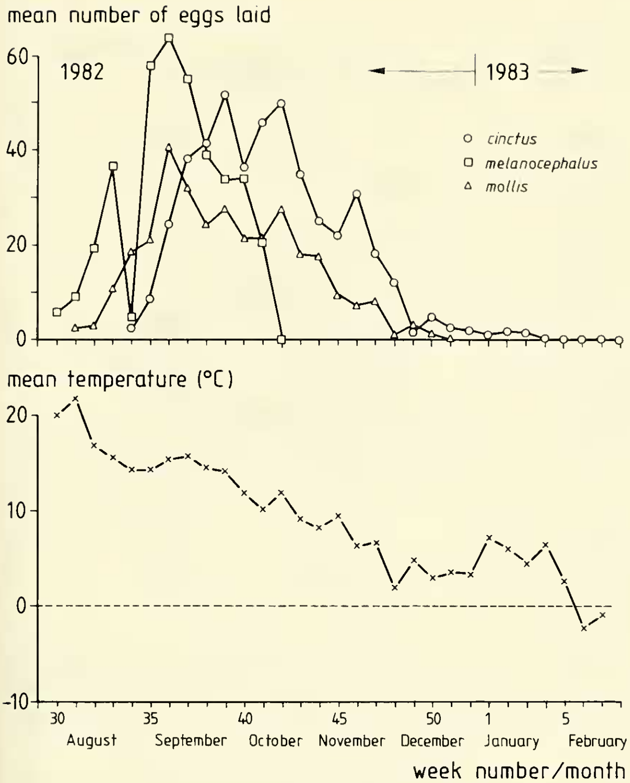


Fig. 14. Mean egg production of *Calathus cinctus* (30 females), *C. melanocephalus* (4 females) and *C. mollis* (17 females) and mean weekly temperatures in 1982/1983 under outside conditions.

here as the period in which the mean number of eggs in the ovaries is 10 or more, fell between the first week of August and the third week of October (table 10). Forty females (24.2 %) were classified as old females, reproducing for the second year. Comparable data for *melanocephalus* collected at the same site resulted in a main reproductive period between the third week of July and the first week of October and 16 % old females (table 10), of which only a single female caught on 13 October was not or no longer reproductive.

Calathus mollis was not studied in detail in this respect but hand catches on the West Frisian Island of Ameland on 27 May 1981 comprised old beetles only (29), whereas on 28 June 1979 about 12 % of the 248 beetles collected at the same site were just emerged tenerals. These data suggest a similar type of age composition of populations of this species.

In the laboratory a small part of the females of all three species kept individually even survived a second hibernation period and laid eggs during a third year.

Outdoor breeding experiments carried out in 1981 and 1982 also gave an impression of the reproductive period of the three species (table 11). Also in these experiments *melanocephalus* showed an earlier start and finish of the egg-laying period than both *cinctus* and *mollis*. Differences between the results for the two years are attributed to different temperature conditions. In 1981, for instance, all females stopped egg production in the first third of December because of a sudden frost period (fig. 13). Due to the later start, *cinctus* and *mollis* suffered more from this event than *melanocephalus*. Under the more favourable weather conditions of 1982/1983 *melanocephalus* showed about the same reproduction period, whereas both *cinctus* and *mollis* were able to prolong their reproduction periods substantially under these conditions (fig. 14).

Data on egg production and larval development of the three species in relation to wing development, temperature and availability of food will be published elsewhere.

Daily rhythms. – Information about the daily activity of the species was derived from a small experiment in which the egg production was estimated every two hours under fixed temperature and daylength conditions. On 14 September 1981 eight reproductive females of *cinctus*, *melanocephalus* and *mollis*, collected at Ameland on 14 July, were transferred from the outdoor breeding house to an incubator adjusted at 19° C and a daylength of 14.75 hours (6.15-19.00 h). They were kept there with males in single pairs for three days. In all three species egg production took place mainly during the dark hours (18.30-6.30 h); a very few eggs were also laid during the early morning hours (table 12).

Emergence of adults. – The outdoor breeding experiments also gave an impression of the emergence period of the adults (table 13). In 1982 almost all *cinctus*, *melanocephalus* and *mollis* emerged in the first two thirds of June, and in 1983 in the latter half of the same month. Van Dijk (1973) trapped teneral females of *melanocephalus* in the field as well as in enclosure experiments during a short period from 15 June onwards. Samples of *cinctus* and *mollis* collected on 28 June 1979 on the West Frisian Island of Ameland consisted of 75 % (102 of 138 specimens) and 11.7 % (26 of 248 specimens) tenerals respectively.

Feeding. – Feeding behaviour and prey spectrum of *melanocephalus* were studied by Hengeveld (1980) by identifying food remains in the gut contents of beetles trapped in the field and killed instantly. From the diet components found, it appeared that *melanocephalus* is a polyphagous, but not exclusively carnivorous species (see also Melber 1983). Similar results were found by Smit (1957), Skuhravý (1959) and Hengeveld (1980) for the closely related *Calathus ambiguus* (Paykull), *C. erratus* Sahlberg and *C. fuscipes* (Goeze).

Dispersal. – Den Boer (1977) developed criteria to classify carabid beetles in three dispersal groups using data on wing development, wing-morph frequencies and actual flight (catches of flying beetles in window traps). A-species are those with a relatively low power of dispersal (monomorph brachypterous or wing-polymorphic species with a very low frequency (< 1%) of macropterous beetles). B-species have a relatively high power of dispersal due to their capability of flight (macropterous and wing-polymorphic species caught in window traps, see also van Huizen 1980), whereas C-species are the remaining species (macropterous or wing-polymorphic with a high frequency of macropterous beetles, but never or rarely caught flying) with uncertain dispersal power.

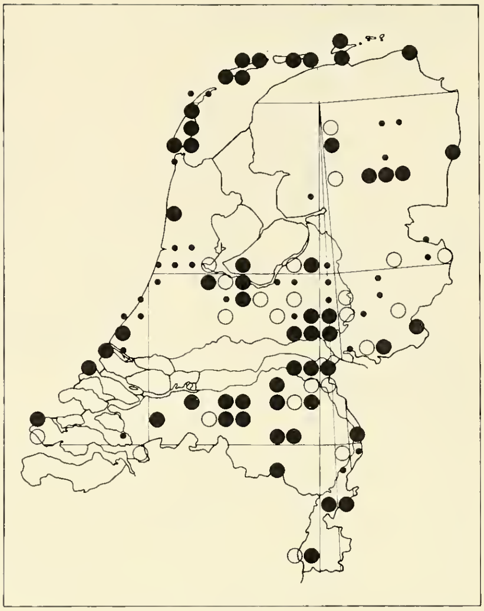


Fig. 15. Distribution of *Calathus cinctus* in The Netherlands. Symbols on this and the following maps: open circles: recorded before 1930 only; small dots: recorded between 1930 and 1960; large dots: recorded since 1960.

The wing-dimorphic *cinctus* was caught in window traps (van Huizen 1980; den Boer et al. 1980) and consequently belongs to the group of B-species (van Dijk 1986).

The wing-dimorphic *melanocephalus* and the monomorph macropterous *mollis* were never caught flying, but laboratory-bred beetles of both species developed flight muscles and flew frequently in a laboratory test (to be published elsewhere). For the time being both species therefore have to be considered C-species. Den Boer (1977)

Table 13. Emergence of adult beetles in outdoor breeding experiments. N: number of beetles.

		Species					
		cinctus		*melanocephalus*		*mollis*	
Year	Decade	N		N		N	
1982	1-10 June	3	(1.8 %)	113	(43.3 %)	158	(98.7 %)
	11-20 June	136	(80.5 %)	101	(38.7 %)	2	(1.2 %)
	21-30 June	29	(17.2 %)	40	(15.3 %)	–	–
	1-10 July	1	(0.6 %)	7	(2.7 %)	–	–
1983	1-10 June	–	–	–	–	–	–
	11-20 June	69	(53.9 %)	12	(34.3 %)	32	(68.1 %)
	21-30 June	58	(45.3 %)	23	(65.7 %)	15	(31.9 %)
	1-10 July	1	(0.8 %)	–	–	–	–

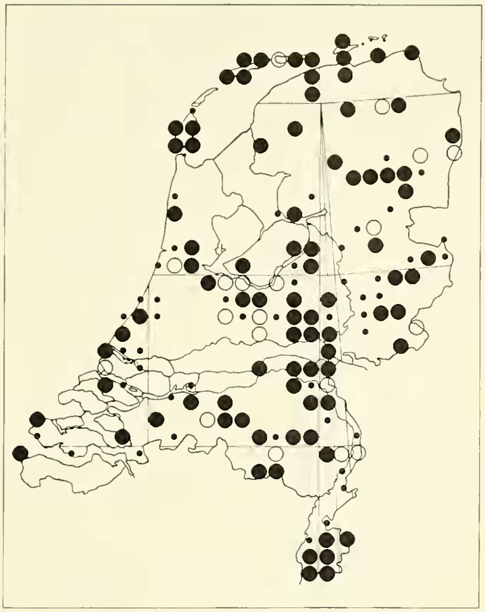


Fig. 16. Distribution of *Calathus melanocephalus* in The Netherlands.

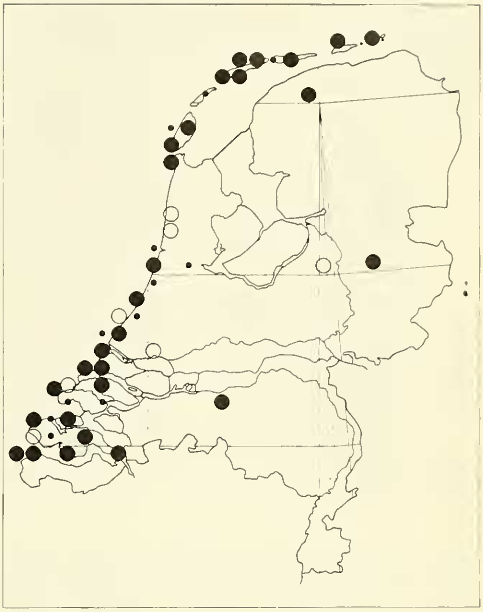


Fig. 17. Distribution of *Calathus mollis* in The Netherlands.

and van Dijk (1986) treated *melanocephalus* as A-species, based on the extremely low frequency of macropterous beetles in populations investigated in the Dutch province of Drenthe (0.23 %). Populations in the recently reclaimed Flevopolders, however, showed a considerable higher freqency of macropterous beetles (25-40%: den Boer 1970; Aukema 1986).

During breeding the flight muscles are autolysed in these species and flight only occurs before breeding. Data on the development of flight muscles and the occurrence of actual flight from the field and from breeding experiments in relation to temperature and availability of food will be treated elsewhere (Den Boer et al. (1980) already gave some preliminary data for *cinctus*).

Distribution

Distribution in The Netherlands

Available data were used to prepare distribution maps on the UTM 10 × 10 square km scale as used by the European Invertebrate Survey in The Netherlands (figs. 15-17).

Calathus cinctus (fig. 15) and *C. melanocephalus* (fig. 16) are widely distributed over the whole country, whereas *C. mollis* (fig. 17) is almost restricted to the coastal dune region, with only a few inland populations on blown sands or other large sand deposits. Desender (1985, 1986) and Moncel (1972) published comparable maps and data for Belgium and France respectively.

A closer examination of the data of *cinctus* (fig. 15) shows, that this species has been caught regularly in The Netherlands since 1864 (Overveen, vi, 1 female, leg. J. Kinker, coll. Zoölogisch Museum, Amsterdam). For *melanocephalus* and *mollis* respectively the first records are Overveen, x.1864, J. Kinker, 1 male (coll. Zoölogisch Museum, Amsterdam) and Driehuizen, 23.vii.1882, 1 male (coll. Zoölogisch Museum, Amsterdam).

Time-trends in the number of 10 × 10 km squares occupied per decade by the three species were estimated according to the method of Turin & den Boer (1988). Fig. 18 shows the time-trends after correction of the number of occupied squares for differences in collecting intensity between the decades (table 14). *Calathus melanocephalus* shows a significantly increasing time-trend, whereas both *cinctus* and *mollis* show rather indifferent time trends (fig. 18). When considering the 20th century only (table 14: decades 4-12) all three species show negative correlation coefficients, but only in the case of *cinctus* was this significant, largely due to the high number of squares occupied in the years 1910-1930.

Ranges

Concerning their general distribution, revision of material on a larger scale is necessary to get a

Table 14. Number of 10 x 10 km squares occupied per decade by *Calathus cinctus*, *C. melanocephalus* and *C. mollis*. TO: total number of squares occupied by all carabid species per decade; F: correction factor calculated from the total number of squares covering The Netherlands (F=448/TO); O: actual number of occupied squares; OF: corrected number of occupied squares (OF=O★F).

Decade				*cinctus*		*melanocephalus*		*mollis*	
Nr	Years	TO	F	O	OF	O	OF	O	OF
1	1870 - 1879	72	6.22	2	12	0	0	2	12
2	1880 - 1889	81	5.53	1	6	1	6	3	17
3	1890 - 1899	108	4.15	5	21	7	29	5	21
4	1900 - 1909	150	3.03	16	48	18	55	6	18
5	1910 - 1919	192	2.35	26	61	24	56	11	26
6	1920 - 1929	214	2.10	22	46	28	59	9	19
7	1930 - 1939	213	2.10	18	38	29	61	15	32
8	1940 - 1949	246	1.82	12	22	26	47	7	13
9	1950 - 1959	264	1.70	16	27	35	59	13	22
10	1960 - 1969	312	1.44	9	13	20	29	10	14
11	1970 - 1979	336	1.33	23	31	35	47	12	16
12	1980 - 1989	350[1])	1.28	21	27	33	42	9	11

[1]) Estimated value. Up till now 14714 records from 321 squares were recorded, but many have to be added (H. Turin, personal communication)

reliable picture (the data in Turin (1981) are only based on literature). In the Dutch collections mentioned and/or in the collections of the British Museum (Natural History), London, the Zoologisches Museum, Berlin, the Zoologische Staatssammlung, München, and M. Baehr, München, I have seen material from the following localities:

C. cinctus: South-England (south of the line River Seven -The Wash), Wales, Ireland, The Netherlands, Belgium, Germany, Poland, the Baltic States (Estonia), Russia, France, Spain, Sardinia, Corsica, Italy, Sicily, Malta, Yugoslavia, Austria, Hungary, Romania, Bulgaria, Albania, Greece, Cyprus, Turkey, Crimea, Ukraine, the Caucasus, Iran, Syria, Israel and Morocco;

C. melanocephalus: Finland, Sweden, Norway, Denmark, Iceland, England, Scotland, Wales, Ireland, The Netherlands, Belgium, Luxembourg, Germany, Poland, the Baltic States (Estonia), France, Spain, Sardinia, Corsica, Italy, Sicily, Yugoslavia, Switzerland, Austria, Hungary, Romania, Albania, Greece, Turkey, Ukraine and the Caucasus;

C. mollis: Denmark, England, Wales, Scotland, Ireland, The Netherlands, Belgium, Germany (the East Frisian Islands), France, Portugal, Spain, Mallorca, Italy, Sicily, Yugoslavia, Greece, Turkey, Gibraltar, Malta, Algeria and Morocco.

Lindroth (1986) indicated the occurrence of *cinctus* in South-Sweden and Denmark (see also Bangsholt 1983) and of *mollis* in Norway. Since Lindroth listed the right combination of characters for both taxa, his findings, although not confirmed, are considered reliable. Anderson (1987, in litt. 1990) furthermore found *cinctus* to be sporadically distributed around the Irish coast south of the line from the Shannon Estuary to Dublin.

Calathus melanocephalus obviously has a Euro-

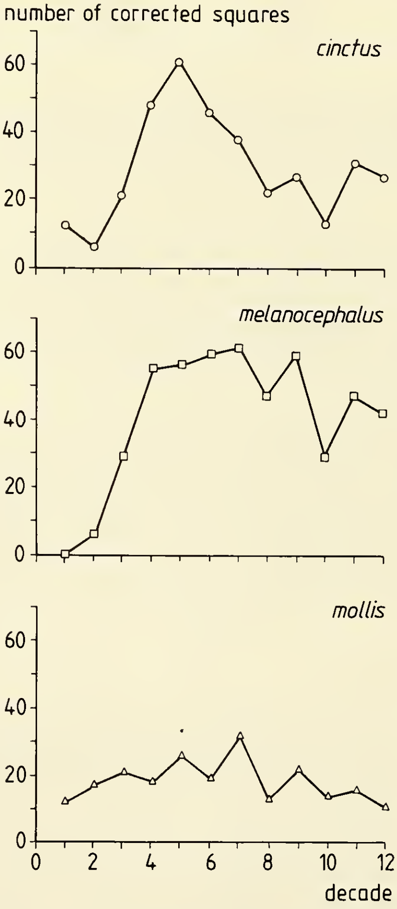


Fig. 18. Plots of the corrected time trends of *Calathus cinctus*, *C, melanocephalus* and *C. mollis*; decades: 1870-1879 (1), 1880-1889 (2), 1890-1899 (3), etc.

pean distribution, ranging from Iceland and Scandinavia in the North to the Mediterranean in the South. It is the only species of this group also occurring at higher altitudes in mountain areas. The subspecies *alpinus* Dejean is restricted to the eastern Alps (Koch 1989). Ball & Negre (1972) list a probably introduced specimen of *melanocephalus* from North America.

Calathus cinctus does not occur as far north as *melanocephalus*, but in the Mediterranean it reaches further south, occurring as far as Morocco and Algeria in the west and Syria and Iran in the east.

Calathus mollis seemingly is restricted to the Atlantic and Mediterranean coastal areas.

DISCUSSION

The establishment of *Calathus* (*Neocalathus*) *cinctus* as a good species has solved a major identification problem in the genus *Calathus*, although even now long winged females of *cinctus* are difficult to distinguish from those of *mollis*. On the other hand, a new problem arises in the interpretation of existing literature on the species of the *melanocephalus*-group. It is quite clear from the data presented here that *cinctus*, although in literature still considered to be mainly distributed in Eastern Europe (southeast and east of the river Weser) (Lienemann 1981; Koch 1989), is a very common species in Western Europe too. For instance in England *cinctus* was already present at the time of Stephens, because in his collection, bought in 1853 by the British Museum (Natural History), London, and kept in its original state (Hammond 1972) four out of the 13 specimens in the box of *melanocephalus* belong to *cinctus* (1 male and 3 females, all short winged). Furthermore Jeannel (1942) already indicated the occurrence of *cinctus* in western France (Vendée).

Lindroth (1949) used data on wing development in *Calathus mollis* as one of the main illustrations for his theory of postglacial recolonization of Fennoscandia. Although Lindroth indicated in the same publication that there were two taxa involved, his data were never revised. Also the data from the following studies will have to be reconsidered concerning species identity: for larval taxonomy (Kurka 1971: description of larval stages of *melanocephalus* and *mollis*), for diagnostics of eggs (Luff 1981: characteristics of the eggs of *melanocephalus* and *mollis*), for chromosome numbers (Serrano 1981: chromosome numbers of *melanocephalus* ($n=37$) and *mollis* ($n=39$)), for population dynamics (Gilbert 1956: population dynamics of *melanocephalus* and *mollis* in the coastal dunes of the Isle of Anglesey where, as we know now, all three species occur), for the occurrence in agricultural fields (Luff 1987: only references for the occurrence of *melanocephalus*), for flight observations (Palmén 1944: long-winged *melanocephalus* washed ashore on the southwestern coast of Finland; Honek & Pulpán 1983: *melanocephalus* caught in a light trap), and for bionomics and breeding (Kurka 1972: *melanocephalus* and *mollis*).

Table 15. Spearman rank correlation coefficients between the corrected number of squares occupied and the decade rank

Species	All decades	20th Century[1])
cinctus	+0.21	-0.74*
melanocephalus	+0.72*	-0.54
mollis	-0.20	-0.60

*) $0.02 < P < 0.05$

[1]) decades 4-12 of table 14

CONCLUSIONS

1. *Calathus* (*Neocalathus*) *cinctus* Gemminger & Harold is considered a good species, reproductively isolated from both the closely related *C.* (*N.*) *melanocephalus* (Linnaeus) and *C.* (*N.*) *mollis* (Marsham).
2. The species of this so-called *melanocephalus* group can be distinguished from each other reliably only on the basis of the shape of the elytra, coloration characters and the shape of the right parameres.
3. Morphological measurements and ratios are not useful in identifying these species.
4. Both *cinctus* and *melanocephalus* are wing-dimorphic with either fully developed wings (of about 1.5 times the length of the elytra) or reduced wings (of about 0.5 times the length of the elytra), whereas Dutch *mollis* always are macropterous.
5. According to the subdivision in habitat groups of Den Boer (1977) *cinctus* is classified as H-species (species preferring localities significantly influenced by human activities), *melanocephalus* as mainly a species of heath and peatmoor (F-species) and *mollis* as E-species (species of blown sands/dunes).
6. The species are night-active autumn breeders. *Calathus melanocephalus* reproduces earlier and during a shorter period in the season than *cinctus* and *mollis*.
7. Age-composition of populations of *cinctus* and *mollis* resembles those of *melanocephalus* (not only larvae, but also a varying part of the adult beetles overwinters and reproduces for a second time).
8. Concerning dispersal power *cinctus* is classified as a good disperser (B-species sensu Den Boer, 1977), whereas *melanocephalus* and *mollis* are considered C-species (species with uncertain

dispersal power) by lack of information on actual flight.

9. All three species are common in The Netherlands and were so during the 20th century. Both *cinctus* and *melanocephalus* are well distributed all over the country, whereas *mollis* is limited to coastal dunes and a few inland blown sands or other large sand deposits.
10. All three species are mainly european in distribution, with *melanocephalus* reaching further north and occurring also at higher altitudes in mountain areas, *cinctus* reaching further south and *mollis* limited to coastal areas in the Atlantic and mediterranean area.

Acknowledgements

Many thanks are due to P. J. den Boer, J. C. van Lenteren and M. L. Luff for critical comments on the manuscript, to Th. S. van Dijk, Y. Jongema, A. Spee, T. H. P. van Huizen, M. G. J. Oude Wesselink, J. Popping and H. Lindenschot for their assistance during practical work, to P. Hammond and M. J. D. Brendell (British Museum (Natural History), London), M. Baehr (Zoologische Staatssammlung, München), F. Hieke (Zoologisches Museum, Berlin), J. Krikken (Rijksmuseum van Natuurlijke Historie, Leiden), B. Brugge and W. Hogenes (Zoölogisch Museum, Amsterdam) and J. G. Rozeboom (Department Entomology, Agricultural University, Wageningen) for the loan of specimens and to all those mentioned under material for supplying additional material. M. L. Luff improved the English text.

References

Anderson, R., 1987. Some uncommon Carabidae (Coleoptera) from South Dublin/Wicklow. – Irish Naturalist Journal 22: 259-260.

Aukema, B., 1986. Wing lengrh determination in relation to dispersal by flight in two wing dimorphic species of *Calathus* Bonelli (Coleoptera, Carabidae). – In: Carabid beetles. Their adaptations and dynamics (P. J. den Boer, M. L. Luff, D. Mossakowski and F. Weber eds.): 91-99. Fischer, New York.

Aukema, B., 1990. The nomenclature of the *melanocephalus* group of the genus *Calathus* (Coleoptera: Carabidae). – Entomologische Berichten, Amsterdam 50: 143-145.

Aukema, B. & M. L. Luff, 1990. *Carabus mollis* Marsham, 1802 (currently *Calathus mollis*; Insecta, Coleoptera): proposed conservation of the specific name. – Bulletin of Zoological Nomenclature 47, in press.

Baars, M. A. & Th. S. van Dijk, 1984. Population dynamics of two carabid beetles at a Dutch heathland II. Egg production and survival in relation to density. – Journal of Animal Ecology 53: 389-400.

Ball, G. E & J. Negre, 1972. The taxonomy of the nearctic species of the genus *Calathus* Bonelli (Coleoptera, Carabidae). – Transactions of the American entomological Society 98: 413-533.

Bangsholt, F., 1983. Sandspringernes og løbebillernes udbredelse og forekomst i Danmark ca. 1830-1981 (Coleoptera: Cicindelidae and Carabidae). – Dansk faunistik Bibliotek 4: 1-271.

Boer, P. J. den, 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). – Oecologia 4: 1-28.

Boer, P. J. den, 1977. Dispersal power and survival. Carabids in a cultivated countryside. – Miscellaneous Papers Landbouwhogeschool Wageningen 14: 1-190.

Boer, P. J. den, T. H. P. van Huizen, W. den Boer-Daanje, B. Aukema & C. F. M. den Bieman, 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae). – Entomologia Generalis 6: 107-134.

Desender, K., 1985. Carabid beetles new for the Belgian Fauna. – Bulletin et Annales de la Société (Royale) Entomologique de Belgique 121: 69- 74.

Desender, K., 1986. Distribution and ecology of carabid beetles in Belgium (Coleoptera, Carabidae). 4. Species 153-217. – Studiedocumenten koninklijk Belgisch Instituut voor Natuurwetenschappen 30: 1-23.

DeZordo, I., 1979. Phänologie von Carabiden im Hochgebirge Tirols (Obergurgl, Österreich) (Insecta: Coleoptera). – Bericht Naturwissenschaftlich-Medizinischen Vereins Innsbruck 66: 73-83.

Dijk, Th. S. van, 1972. The significance of the diversity in age composition of *Calathus melanocephalus* L. (Col., Carabidae) in space and time at Schiermonnikoog. – Oecologia 10: 111-136.

Dijk, Th. S. van, 1973. The age-composition of populations of *Calathus melanocephalus* L. analysed by studying marked individuals kept in fenced sites. – Oecologia 12: 213-240.

Dijk, Th. S. van, 1978. *Calathus mollis erythroderus* Gemminger & Harald in Drenthe (Coleoptera, Carabidae). – Entomologische Berichten, Amsterdam 38: 151-153.

Dijk, Th. S. van, 1979a. On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coerulescens* L. (Coleoptera, Carabidae). – Oecologia 40: 63-80.

Dijk, Th. S. van, 1979b. Reproduction of young and old females in two carabid beetles and the relationship between the number of eggs in the ovaries and the number of eggs laid. – In: P. J. den Boer, H.-U. Thiele & F. Weber (eds). On the evolution of behaviour in carabid beetles – Miscellaneous Papers Landbouwhogeschool Wageningen 18: 167-183.

Dijk, Th. S. van, 1986. Changes in the carabid fauna of a previously agricultural field during the first twelve years of impoverishing treatments. – Netherlands Journal of Zoology 36: 413-437.

Forsskåhl, B., 1972. The invertebrate fauna of the Kilpisjärvi area, Finnish Lapland. 9. Carabidae, with special notes on ecology and breeding biology. – Acta Societas Fauna Flora Fennica 80: 99-119.

Freude, H., 1976. Adephaga I. – Die Käfer Mitteleuropas 2: 1-302.

Friederichs, K., 1907. Über Verbreitung und Lebensweise einiger Käfer. – Archiv Freunde Naturgeschichte Mecklenburg' 61: 48-60.

Gersdorf, E., 1937. Ökologisch-faunistische Untersuchungen über Carabiden der mecklenburgische Landschaft. – Zoologische Jahrbücher für Systematik, Geographie und Biologie der Tiere 70: 17-86.

Gilbert, O., 1956. The natural histories of four species of *Calathus* (Coleoptera, Carabidae) living on sand dunes in Anglesey, North Wales. – Oikos 7: 22-46.

Hammond, P. M., 1972. On the type material of Staphylinidae (Col.) described by T. Marsham and J. F. Stephens. – Entomologist's Gazette 23: 129-135.

Hengeveld, R., 1980. Polyphagy, oliphagy and food specialization in ground beetles (Coleoptera, Carabidae). – Netherlands Journal of Zoology 30: 564-584.

Honek A. & J. Pulpán, 1983. The flight of Carabidae (Coleoptera) to light trap.- Věstnik ceskoslovenské Společnosti zoologické 47: 13- 26.

Huizen, T. H. P. van, 1980. Species of Carabidae in which the occurrence of dispersal by flight of individuals has been shown. – Entomologische Berichten, Amsterdam 40: 167-168.

Jeannel, R., 1942. Coléoptères Carabiques. – Faune de France 40: 572- 1173.

Koch, K., 1989. Ökologie. I.- Die Käfer Mitteleuropas: 1-440.

Kurka, A., 1971. Larvae of the Czechoslovak species of the genus *Calathus* Bonelli (Coleoptera, Carabidae). – Acta entomologica bohemoslovaca 68: 233-262.

Kurka, A., 1972. Bionomy of the Czechoslovak species of the genus *Calathus* Bon., with notes on their rearing (Coleoptera: Carabidae). – Věstnik ceskoslovenské Společnosti zoologické 36: 101-114.

Lienemann, K., 1981. *Calathus erythroderus* Gemminger et Harold 1868 (Coleoptera, Carabidae) neu im Rheinland. – Decheniana 134: 176.

Lindroth, C. H., 1943. Zur Systematik fennoskandischer Carabiden. – Entomologisk Tidskrift 64: 1-68.

Lindroth, C. H., 1945. Die Fennoskandischen Carabidae. Eine tiergeografische Studie. 1. Spezieler Teil. – Göteborgs Kungliga vetenskaps- och vitterhetssamhälles Handlingar 6, Ser. B 4 (1): 1-709.

Lindroth, C. H., 1949. Die Fennoskandischen Carabidae. 3. Allgemeiner Teil. – Göteborgs Kungliga vetenskaps- och vitterhetssamhälles Handlingar 6, Ser. B 4 (3): 1-911.

Lindroth, C. H., 1974. Coleoptera, Carabidae. – Handbooks for the identification of British Insects 4 (2): 1-148.

Lindroth, C. H., 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica 15 (2): 233-497.

Luff, M. L., 1981. Diagnostic characters of the eggs of some Carabidae (Coleoptera). – Entomologica scandinaviae, Supplement 15: 317-327.

Luff, M. L., 1987. Biology of polyphagous ground beetles in agriculture. – Agricultural Zoology Reviews 2: 237-278.

Melber, A., 1983. Calluna-Samen als Nahrungsquelle für Laufkäfer in einer nordwestdeutschen Sandheide (Col.: Carabidae). – Zoologische Jahrbücher für Systematik 110: 87-95.

Mols, P. J. M., Th. S van Dijk & Y. Jongema, 1981. Two laboratory techniques to separate eggs of carabids from a substrate. – Pedobiologia 21: 444-445.

Moncel, J., 1972. A propos de *Calathus mollis* (Col. Carabidae) et de sa variété erythroderus. – l'Entomologiste 28: 26-30.

Palmén, E., 1944. Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor. – Annales Zoologici Societas Zoologicae- Botanicae Fennicae, Vanamo 10: 1-262.

Refseth, D., 1988. Annual pattern of activity, reproduction and development in some Norwegian Carabidae (Col.). – Fauna norvegiae Ser. B 35: 21-30.

Schatzmayr, A., 1937. I *Calathus* d'Europa. – Publicazioni del Museo Entomologico 'Pietro Rossi' Duino 2: 1-50.

Serrano, J., 1981. Chromosome numbers and karyotypic evolution of Caraboidea. – Genetica 55: 51-60.

Skuhravý, V., 1959. Die Nahrung der Feldcarabiden. – Acta Societas entomologicae ceskoslovenské 56: 1-18.

Smit, H., 1957. Onderzoek naar het voedsel van *Calathus erratus* Sahlb. en *Calathus ambiguus* Payk. aan de hand van hun maaginhouden. – Entomologische Berichten, Amsterdam 17: 199-209.

Thiele, H.-U., 1977. Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour: i-xvii, 1-369. – Berlin.

Turin, H., 1981. Provisional checklist of the European groundbeetles (Coleoptera: Cicindelidae & Carabidae). – Monografieën Nederlandse entomologische Vereniging 9: 1-249.

Turin, H., J. Haeck & R. Hengeveld, 1977. Atlas of the carabid beetles of The Netherlands. – Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde (2) 68: 1-228.

Turin, H. & P. J. den Boer, 1988. Changes in the distribution of carabid beetles in The Netherlands since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). – Biological Conservation 44: 179-200.

Vereshchagina, T. N., 1985. The genus Calathus Bon. (Coleoptera, Carabidae) in the USSR. – Entomological Review 63: 75-94.

Vlijm, L & Th. S. van Dijk, 1967. Ecological studies on carabid beetles. II. General pattern of population structure in *Calathus melanocephalus* (Linn.) at Schiermonnikoog. – Zeitschrift für Morphologie und Ökologie der Tiere 58: 396-404.

Vlijm, L., Th. S. van Dijk & S. Y. Wijmans, 1968. Ecological studies on carabid beetles. III. Winter mortality in adult *Calathus melanocephalus* (Linn.). Egg production and locomotory activity of the populations which has hibernated. – Oecologia 1: 304-314.

Wiebes-Rijks, A. A., 1959. Het onderscheid tussen *Calathus melanocephalus* L. en *Calathus mollis* Marsh. (Coleoptera, Carabidae). – Entomologische Berichten, Amsterdam 19: 248-253.

Received: 13 February 1990
Accepted: 16 August 1990